SOME INVESTIGATIONS OF THE WATER RELATIONS OF LICHENS[1]

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At intervals during the summers of 1941 and 1942 the writers collected samples of lichens at various times of day from a southwest facing sandstone cliff in Hocking County, Ohio, and measured the water content. The purpose of these periodic measurements was to find out when water absorption occurred, where the water came from, and when it was lost. Concurrent measurements of the humidity of the air adjacent to the plants and of the temperature of the air and plants were made with a view toward possible correlation of these data with the moisture data.

FIG. 1. *Gyrophora dillenii* (right center) and *Umbilicaria pustulata* (left center), about one-half natural size.

The lichens chosen for investigation were *Gyrophora dillenii* (Tuck.) Mull. Arg. and *Umbilicaria pustulata* (L.) Hoffm. (Fig. 1). These lichens occur together on the Blackhand sandstone cliff walls of Neotoma, a tributary valley of Clear Creek, Hocking County, in sufficient numbers to permit such an investigation. Gyrophora is a large leathery lichen, dark greenish brown above with a black felt-like mass of rhizoids beneath. The plant is attached to the rock substrate by a short tough umbilicus. Umbilicaria is a smaller thinner lichen than gyrophora, light brown in color with wart-like pustules above and no rhizoids beneath. The plant is also fastened to the substrate by a short umbilicus.

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Experimental data concerning the water relations of lichens are not numerous and are of limited pertinence to our problem. It has been recognized that most lichens do not normally contain much water, that some specimens when moistened attain fresh weights three to four times their dry weights, and that probably some species living in desert and other arid habitats are dependent on the atmosphere and dew for available water. Smith (1921), in a review of the literature to that time, reports that lichens can endure almost complete desiccation during long drought periods. They absorb water over their entire surface and water may be held for some time by rhizoids and gradually absorbed. Heugebauer (1939) studied the water relations of several species of *Parmelia* and of *Usnea dasypoga* and reported differences in rates of water loss and in total amount of water held. Lundegardh (1931) suggests that on naked rock surfaces only small slowly growing plants such as algae and lichens can withstand the periodic desiccation. Weaver and Clements (1938) assert that lichens flourish during periods of wet weather and remain in a state of desiccation for very long periods during drought.

MATERIALS AND METHODS

Samples of lichens were collected in the field, placed in glass bottles with plastic screw-caps, and transported as soon as possible to the laboratory for fresh weight and 103° C. oven-dry weight determinations. Water content is expressed as per cent of the oven-dry weight. It was recognized that some non-uniformity in water content among plants in the same general habitat would probably exist and care was taken to reduce this sampling error by taking large samples consisting of small pieces from many plants. Statements about the water content of intact plants at any particular time are based on samples taken at that stated time. Humidity determinations were made with a Friez aspirating psychrometer. Temperature measurements were made with a Leeds and Northrup portable potentiometer and copper-constantan thermocouples inserted into the lichens or exposed to the air.

FIELD EXPERIMENTS

The first experiment consisted of taking samples of both plants at intervals for a twenty-four hour period. The data are shown in Table I.

TABLE I

DATA OF JUNE 28–29, 1941

Solar Time	Per Cent Water		Temp. in °C.	
	Umbilicaria	Gyrophora	Air	Lichen
1:30 P. M.	18.7	18.6	34.4	32.5
3:30 P. M.*	123.1	365.0	27.2	33.2
5:30 P. M.	37.9	50.1	28.2	32.5
5:30 A. M.	56.9	53.3	22.8	25.5
9:30 A. M.	58.3	44.9	28.6	30.0
11:30 A. M.	28.2	17.9	31.4	38.0
1:30 P. M.	24.0	13.6	28.3	32.0

*Thunder-showers of 0.2 in. between 2:10 P. M. and 2:50 P. M.

The high water content of the samples following the forty minutes of thunder-showers and the rapidity with which much of the water was lost as evidenced by the succeeding samples should be noted. Later laboratory work showed that the water content of gyrophora plants in equilibrium with a saturated atmosphere at

30° C. was 92 per cent. Hence much of the water in the gyrophora plants at 365 per cent water content must have been loosely held on the plant surfaces, not absorbed internally, and evaporated rapidly from the plants. The rhizoids of gyrophora would hold much more water on the surface of the plant than would be held in umbilicaria.

For comparison with Table I, data obtained at a later date are presented in Table II. No rain had fallen in the valley for several days prior to the date of collection.

TABLE II

DATA OF JULY 5-6, 1941

Solar Time	Per Cent Water		Vapor Pressure	Temp in °C.	
	Umbilicaria	Gyrophora		Air	Lichen
4:30 A. M.	112.3	85.4	12.5	18.3	20.0
10:30 A. M.	44.6	46.3	17.5	23.9	25.0
1:30 P. M.	25.3	25.3	17.5	25.8	28.5
4:30 P. M.	16.3	17.4	18.5	28.3	36.5
4:30 A. M.	100.4	74.3	15.5	19.4	24.0
7:30 A. M.*	113.2	82.1	16.5	19.7	23.0

*Light rain falling.

The evidence of considerable increase in water content in the absence of rain during the night hours should be noted. In all other experiments performed which included samples taken at night, evidence of increase in water content during the night was obtained. These findings indicate that extreme drought periods during the summer in this region are limited for these plants to some of the daylight hours. Results of several nights collections at one hour intervals showed no regularity in the rate of water absorption and no uniformity in the amount of water absorbed from night to night.

In an effort to determine whether the water absorbed at night came from the rock substrate or the atmosphere, several experiments were performed with gyrophora plants. Initial samples were taken in the afternoon. At the same time some specimens were detached from the rock, mounted on paraffined papers, and the papers fastened to the rock surface. The next morning, samples were taken of intact and paper mounted plants. Table III summarizes the data. Station A was a more exposed and higher place on the cliff wall than Station B.

TABLE III

Solar Time, Date and Sample	Per Cent Water, Gyrophora	
	Station A	Station B
2:30 P. M. June 25, 1942, initial sample	22.0	....
4:50 P. M. June 25, 1942, initial sample	....	25.0
4:30 A. M. June 26, 1942, final samples—intact	34.0	39.0
paraffined paper	42.0	35.0
4:30 P. M. August 15, 1942, initial samples	17.0	21.0
4:45 A. M. August 16, 1942, final samples—intact	27.0	30.0
paraffined paper	32.0	37.0

Humidity and temperature measurements during the course of the experiments showed that no dew point temperatures were reached at the plant surface or in the air adjacent. No other visual evidence of dew was noted at points that high above the valley bottom. Since both intact and detached plants mounted on paraffined papers absorbed water overnight in fairly comparable amounts it seems likely that the increase in water content during the night hours was due to the imbibition of water vapor into the plants.

The data of Tables I and II indicate a reduction in water content of these lichens during the daylight hours. Visual and physical evidences of this fact have been experienced by the writers in the field many times. Both plants commonly become brittle and gyrophora curls so that the lower surface is exposed (Fig. 1). More detailed data from an experiment with gyrophora plants that were collected from a tree-shaded habitat dominated almost entirely by this species are presented in Table IV. In Table V are similar data for umbilicaria plants collected from a cliff top station somewhat shaded by a pine tree. These latter plants were collected on what proved to be the hottest day in three summers. Table VI is included to show the water content of umbilicaria plants fully exposed to solar radiation during the warmest part of that day.

TABLE IV

DATA OF JULY 22, 1941

Solar Time	Per Cent Water Gyrophora	Vapor Pressure	Temp in ° C.	
			Air	Lichen
4:30 A. M.	33.9	11.5	15.6	22.5
5:30 A. M.	26.0	11.5	15.6	23.0
6:30 A. M.	33.2	11.5	15.6	22.5
7:30 A. M.	31.8	13.0	17.5	22.0
8:30 A. M.	28.9	15.0	20.3	24.5
9:30 A. M.	29.6	14.5	20.6	25.5
10:30 A. M.	18.9	17.5	23.9	28.0
11:30 A. M.	17.5	16.0	24.4	28.0
12:30 P. M.	18.6	15.5	25.0	28.5
1:30 P. M.	18.2	16.0	26.1	28.0
2:30 P. M.	17.0	15.5	25.3	28.5
3:30 P. M.	16.1	16.5	24.7	27.5
4:30 P. M.	17.6	17.5	23.6	27.5

The water content of both lichens decreased during the morning and early afternoon hours due to the diffusion of water vapor from the plants. Calculations of the adjacent atmospheric vapor pressures from psychometric data show a small increase in atmospheric vapor pressure during those hours. The vapor pressure of water in the lichens, then, must have been increasing to an even greater extent than that of the atmosphere or transpiration could not have occurred during those hours. However, as the water content of the plants decreased, the degree of hydration of the plant material should decrease and the vapor pressure decrease to a point approaching that of the atmosphere. One must account for an increase in vapor pressure of the water in lichens whose water content is decreasing. The temperature data show that the temperature of the lichens was commonly higher than that of the air adjacent; this fact would seem to bear a casual relationship to extended periods of water loss from the plants. The data of Table V and Table VI indicate that the more exposed the plants to direct solar radiation, the higher the plant temperature and the lower the water content. In all of the field work in which samples were taken from several regions of the cliff wall at the same time, the lowest water contents were found in the plants exposed to direct solar radiation. The high plant temperatures existing under such conditions would account at least in part for high plant vapor pressures and steeper vapor pressure gradients between plant and atmosphere, and hence for lower water contents.

TABLE V

DATA OF JULY 26, 1941

Solar Time	Per Cent Water Umbilicaria	Vapor Pressure	Temp. in °C.	
			Air	Lichen
4:30 A. M.	24.8	16.5	21.7	25.5
5:30 A. M.	29.0	18.0	22.2	27.0
6:30 A. M.	20.6	18.0	22.8	27.0
7:30 A. M.	22.5	18.5	25.0	27.0
8:30 A. M.	18.7	20.5	27.2	30.5
9:30 A. M.	18.1	21.5	29.4	34.0
10:30 A. M.	16.4	23.5	30.0	39.0
11:30 A. M.	12.7	22.0	28.9	39.5
12:30 P. M.	13.0	23.0	30.6	42.5
1:30 P. M.	11.3	23.5	35.0	42.5
2:30 P. M.	11.4	....	35.6	38.5
3:30 P. M.	10.7	....	35.3	36.5
4:30 P. M.	10.6	24.5	32.8	33.5

TABLE VI

DATA OF JULY 26, 1941

Solar Time	Per Cent Water Umbilicaria	Vapor Pressure	Temp. in ° C.	
			Air	Lichen
12:30 P. M.	8.4	....	43.5	45.0
1:30 P. M.	6.5	....	40.0	48.5
2:30 P. M.	6.4	....	43.0	50.5
4:30 P. M.	7.8	....	39.0	44.0

DISCUSSION

Evidence of marked diurnal fluctuations in water content of these lichens has been presented. Precipitation water or condensation water may be imbibed by these plants and even held by capillarity. The data show, however, that water absorption of some magnitude may occur between periods of precipitation or condensation. The writers' opinion that the direction and rate of water vapor diffusion will explain fluctuations between rains is supported by the experimental results. The factors of greatest importance in determining the direction and magnitude of vapor pressure gradients between these plants and the atmosphere are temperature differences between plants and atmosphere, and changes in the degree of hydration of the plant tissue as they may affect the vapor pressure of water in the plants.

If an imbibition-transpiration mechanism of the water relations of these lichens is valid, it should be possible to predict changes in water content under controlled conditions. Atmospheres of known vapor pressure may be obtained over sulphuric acid solutions of known density and temperature. Lichens with vapor pressures higher than that of a given atmosphere should lose water to that atmosphere until an equilibrium is established. Lichens with vapor pressures lower than that of a given atmosphere should imbibe water vapor until an equilibrium is established.

Gyrophora plants were brought from the field into the laboratory and samples suspended over sulphuric acid solutions of varying density at constant temperature. By using a large ratio of sulphuric acid solution to plant material and air space, the changes in density of the acid due to loss or gain of water were small. The relationship between the equilibrium vapor pressures and the water contents of the lichen

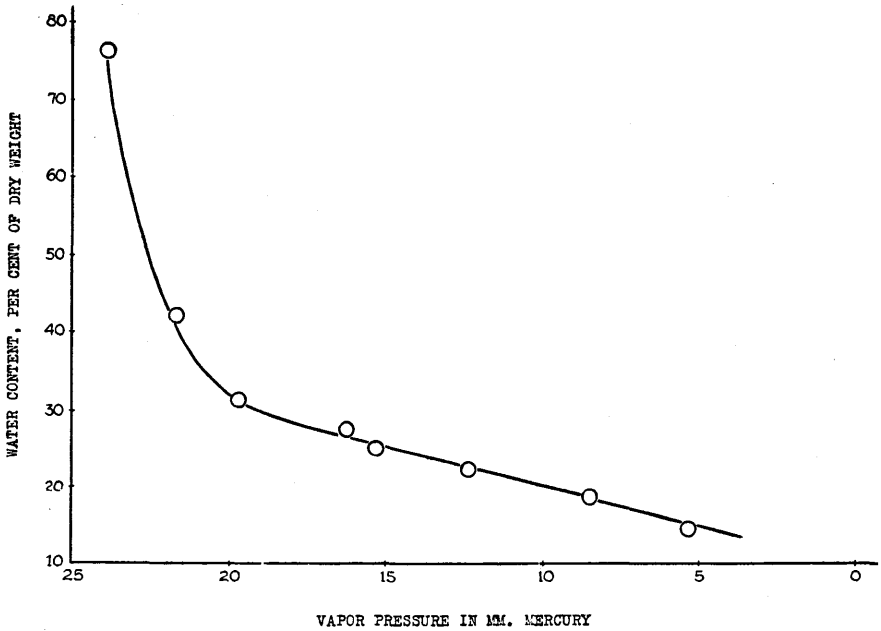

FIG. 2. The water content of samples of *Gyrophora* in equilibrium with sulphuric acid solutions of known vapor pressure at 24° C.

samples is shown in Figure 2. The curved line would represent the path of change in water content of a given sample of gyrophora plants in equilibrium with a saturated atmosphere as it came into equilibrium with sulphuric acid solutions of increasing density and decreasing vapor pressure. The shape of the curve indicates that water above 30% water content is held very loosely and small changes in the equilibrium vapor pressure result in large changes in the percentage water content. At water contents below 30% in this experiment, the water is held more tightly and large changes in the equilibrium vapor pressure result in relatively small changes in the percentage water content.

The results of the experiment substantiate the idea of imbibition of water vapor by these plants and transpiration from them. Attempts to utilize this method to estimate the actual vapor pressures of water in plants in the field by finding the vapor pressure at which no change in weight of the sample occurred, met with technical difficulties. Obviously the temperature of the plants at the time of collection would have to be known and kept constant in order to keep the vapor pressure constant. The temperature of the sulphuric acid solutions would have to be carefully regulated to that of the plants in the atmosphere above. Errors due to uncontrollable variations in these last mentioned factors were too great to make the method useful in the field.

A laboratory experiment was performed to test the influence of solar radiation on the rate of water loss from water saturated plants on the final equilibrium water content. Gyrophora plants were soaked in water for several hours and then suspended in air until water ceased to drip from them. They were spread out on a laboratory table and their fresh weights determined at regular intervals until they reached constant weight. The oven dry weight of the plants was then determined and the fresh weights converted to per cent of water on a dry weight basis. A similar experiment was performed with gyrophora plants spread out

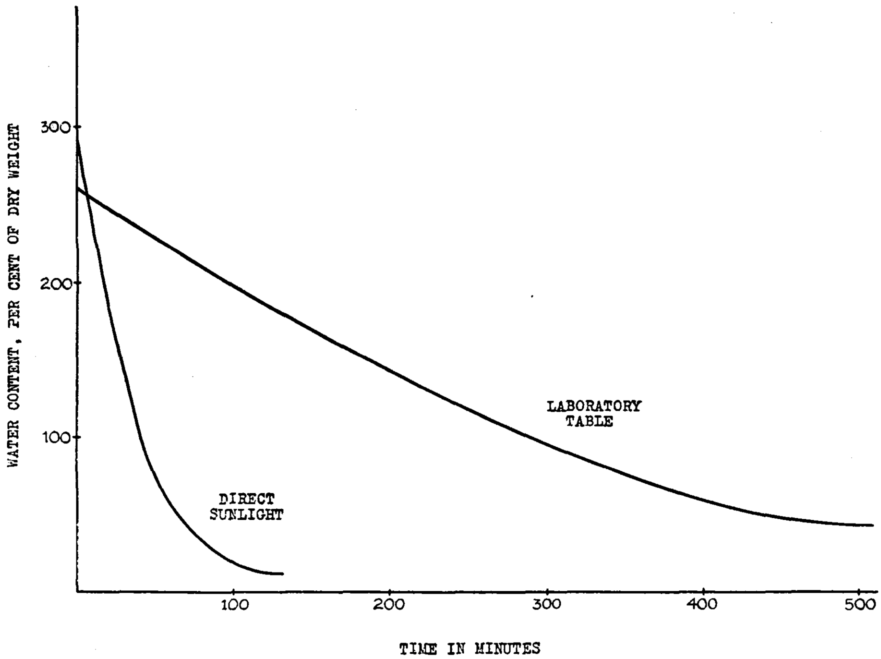

FIG. 3. Drying curves of *Gyrophora* samples indoors on a laboratory table and out-of-doors in direct sunlight.

on a glass plate on the ground outside the laboratory and exposed to solar radiation. The data are presented as drying curves in Figure 3. The slope of the curves indicates relative rates of water loss and the final equilibrium water contents are apparent as the curves flatten out parallel to the abscissa. The influence of solar radiation is apparent on inspection and in agreement with field data.

SUMMARY

Field experiments were performed with two species of lichens growing on the southwest facing cliff walls of a valley in Hocking County, Ohio. Data on the percentage water content on a dry weight basis, plant and air temperatures, and atmospheric humidity were obtained at various intervals during two summers.

The results of these experiments indicate that these plants do not remain in a state of desiccation during periods between rains or dew, but exhibit a marked

diurnal fluctuation in water content. During the daylight hours, particularly in clear weather, the water content decreases due to transpiration. Extended periods of transpiration are possible because the temperature of the plants was found to be commonly higher than that of the air adjacent, especially if exposed to solar radiation. Such temperature differences would cause the occurrence of a vapor pressure gradient from plants to atmosphere even at low water contents of the plants. During the night hours, imbibition of water vapor into the lichens occurs whenever the vapor pressure gradient is from atmosphere to plants. Such a condition may exist when plants at low water content become cooled at night to a temperature close to that of the atmosphere.

Laboratory experiments were performed and the results substantiate the fact that these lichens may gain water vapor by imbibition and lose water vapor by transpiration. The effect of solar radiation on increasing the rate of transpiration and lowering the final equilibrium water content was also demonstrated.

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